SUCCESSIONAL PATTERNS OF THE LOWER MONTANE TREELINE, EASTERN CALIFORNIA

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ABSTRACT

Stand age patterns of pinyon woodlands along the lower montane treeline ecotone (LMTE) in eastern California suggest that prior to European settlement, woodlands were very open (41 trees/ha) and were mostly restricted to xeric topographic settings with shallow, coarse-textured soils. Since European settlement in about 1861, pinyon woodlands have rapidly increased in density, expanded downslope, and invaded more mesic topographic sites.

The lower montane treeline ecotone (LMTE) forms the lower elevation extent of montane vegetation communities in the Intermountain West. In Inyo and Mono Counties the LMTE is dominated primarily by open woodlands of *Pinus monophylla* Torr. and Frem. (single-needle pinyon pine) with an understory of predominantly Great Basin shrub species such as *Artemisia* spp. (sagebrush), bitterbrush (*Purshia* spp.), and rabbitbrush (*Chrysothamnus* spp.) (Vasek and Thorne 1977). The pinyon woodland occurs mostly between 1900 m–2900 m elevation. In the eastern Sierra Nevada, Sweetwater Mountains, and Glass Mountain Ridge, the upper elevations of pinyon grade into montane forests and woodlands of Jeffrey pine (*Pinus jeffreyi*), lodgepole pine (*Pinus murrayana*), and white fir (*Abies concolor*). In the White Mountains and Bodie Hills, a sagebrush shrubland dominates the cover immediately above the pinyon woodlands. In the White-Inyo Range, subalpine woodlands of bristlecone pine (*Pinus longaeva*) and limber pine (*Pinus flexilis*) occur above the upper sagebrush zone (St. Andre et al. 1965; Spira 1991; Vasek and Thorne 1977).

The pinyon woodland in eastern California is unusual in the rarity of Utah juniper (*Juniperus osteosperma*), which commonly codominates with pinyon to form a pinyon-juniper woodland throughout the central Great Basin (West et al. 1978). Utah juniper co-occurs with pinyon in eastern California primarily in the White-Inyo Range where it is largely restricted to sites on alluvial soils (St. Andre 1962; Mooney 1973). Of the 521 trees sampled in this study, only two are Utah juniper, and the remainder are single-needle pinyon.

Throughout the Intermountain and Rocky Mountain west, observers have noted that the lower montane woodlands have been expanding downslope and have become denser within their elevational range since the late 1800's (Cottam and Stewart 1940; Blackburn and Tueller 1970; Burkhardt and Tisdale 1969, 1976; Rogers 1982; Vale 1975). Early observations, historic photographs, and stand age data suggest that lower montane woodlands were formerly savanna-like, with trees restricted to rocky outcrops or steep slopes with coarse-textured soils. Many of these topographic sites with existing trees have subsequently converted to fully-stocked stands while much of the range expansion of pinyon and juniper has been onto gently sloping or valley bottom sites with deeper, finer-textured soils (Cottam and Stewart 1940; Burkhardt and Tisdale 1969, 1976; Miller 1921; Miller and Rose 1995; Phillips 1909; Woodbury 1947).

While the ecology of pinyon and juniper woodlands has been extensively investigated, patterns and processes along the LMTE have received little study. Most previous workers have been concerned with larger-scale relationships of mature woodlands, and so have avoided sampling and describing ecotonal or early successional stands (Koniak 1986; Meeuwig and Cooper 1981; Tausch et al. 1981; Tueller et al. 1979; West et al. 1978). Blackburn and Tueller (1970) described and classified the range expansion of single-needle pinyon and Utah juniper in eastern Nevada, but did not investigate differences in stand age and dominance in relationship to the landscape topography. In this work I present pinyon age and dominance data in relation to topographic settings along the LMTE.

METHODS

The study areas are all within Inyo and Mono Counties, California; and sites were located in the Bodie Hills, Glass Mountain Ridge, the White Mountains, the Sherwin Summit area just east of the Sierra Nevada, and at Tuttle Creek, at the base of the southern Sierra Nevada. Sites were selected where the LMTE occurs in each area. Elevations ranged from 1900-2000 m elevation. Sampling areas were usually small drainage basins. Plots were randomly placed on a variety of topographic positions with a maximum of 50 m elevation difference within a sampling area. At this small scale, it was assumed that soil moisture variation is primarily a

function of soil texture and topographic position, and that the influence of elevation is a constant.

The LMTE is highly interdigitated with respect to topographic position. The woodland is more developed and extends further downslope on topographic convexities, such as ridges, and steep slopes. To measure the influence of topographic position on stand variables, the sampling frame was stratified based on topographic position using the Topographic Relative Moisture Index (TRMI) (Parker 1982). The TRMI is a scalar index (0–60, 0 = most xeric topographic sites, 60 = most mesic) designed for mountainous terrain in the western United States, and offers a way to stratify the landscape into topographic position based on slope angle, configuration, aspect, and position on the slope. Individual plots were placed randomly within each landscape unit, such as valley bottom, ridge top, toe slope, and upper slope. This stratified random sampling process sometimes resulted in the placing of field plots where trees were absent; however, a sampling frame based on vegetative characteristics would not reflect the topographic influence on stands. Each plot was checked visually to insure that it did not include anomalous vegetative cover relative to the rest of the landscape unit.

To examine the hypothesis that pinyon existed as open woodlands primarily on xeric sites prior to European settlement, and then invaded onto mesic sites, I separated the plots into 22 xeric (low TRMI, <30) and 22 mesic (high TRMI, >30) sites. While there is a gradation between xeric and mesic sites, the combined weight of the slope variables (topographic position, slope steepness, and slope configuration) made them more important than aspect in determining whether a site was classified as mesic or xeric. In general, sites described as xeric are mostly located on topographic convexities and steeper slopes, and the mesic sites are located in draws, valley bottoms and other topographic concavities. Soil variables are not incorporated into the TRMI; however, within each study site, there is a strong positive correlation between shallow, coarse-textured soils and xeric sites as determined by the TRMI excluding aspect (Vaughn 1983).

Plots were 30 m × 30 m in all areas except the White-Inyo Range, where 50 m × 20 m plots were used to be consistent with previous field work (St. Andre 1962). All lives trees rooted in the plot >1.5 m height were cored at 30 cm for aging, and all trees were measured for basal area, crown projection area, and height. Understory cover was measured by the line-intercept placement of a 30 m transect through the plot. Percent cover was calculated as the percent distance intersected vertically by the line. In each study area, cross-sections were cut from juvenile trees <1.5 m height to determine the age to coring height. The average age at 30 cm was found to be 12.24 yrs (n = 30), so 12 years were added to the ring count age of each tree. To gain a representation of the age patterns of juveniles <1.5 m height, a simple linear regression equation was used to predict their ages. The best equation to predict age was based on stem radius and tree height (both measured in centimeters) using data from the cross-sectioned trees and cored trees <3 m height. The simple linear regression equation is

$$Age = 8.19(radius) + 0.169(height); n = 122,$$
$$r^2 = 65\%, p < 0.0005.$$

Growth rates are highly variable for immature trees due to their greater sensitivity to soil moisture fluctuations (Barton 1993), variations in overstory canopy shade, and the potential influences of nurse shrubs (Drivas and Everett 1988). Consequently, the predicted ages of juvenile trees are not reliable in determining actual dates of recruitment or seedling establishment, but they do offer a relatively accurate picture for interpreting overall reproductive status of the stand.

Finally, while there is no evidence of historic wood cutting on the sites, such as stumps, and the sampled stands are not within the known woodsheds of historic mining centers in the area, the possibility exists that some mature trees may have been cut for wood use in the past, and are now absent from the stands.

RESULTS AND DISCUSSION

At the LMTE, topographic position explains more variation in pinyon age and dominance patterns than elevation or aspect. Figures 1a and b illustrate tree ages from the 44 plots, and Table 1 summarizes stand age and density data. Of 381 trees aged by ring counts and 140 juvenile ages predicted through linear regression, 23% on all sites, 29% on xeric and 13% on mesic sites, predate European settlement. The mean (and median) tree ages of all sites today is 97.2 (79) years, on xeric sites 106.6 (81) years, and on mesic sites 83.6 (78) years. Currently and in 1861, pinyon stands on xeric sites are significantly older than trees on mesic sites along the LMTE (two-tailed t-test, p < 0.005). There was no difference in statistical significance when ages from cored only, or cored and predicted juvenile ages, were used.

Prior to the establishment of permanent European ranching and mining settlements in Inyo and Mono Counties in 1861 (Chalfant 1933; Sauder 1994), the data suggest that pinyon woodlands were largely restricted to xeric habitats, such as topographic convexities and steep slopes with thin, rocky soils. From stand age reconstructions, xeric sites supported an average of 45 trees/ha in 1861. Draws and other topographic concavities with deeper, finer-textured soils supported 13 trees/ha on average. Today, xeric sites support 156 trees/ha, and mesic sites 107 trees/ha. Estimated average tree ages in 1861, however, show stronger contrasts in tree dominance: 41 years in mesic sites, with one

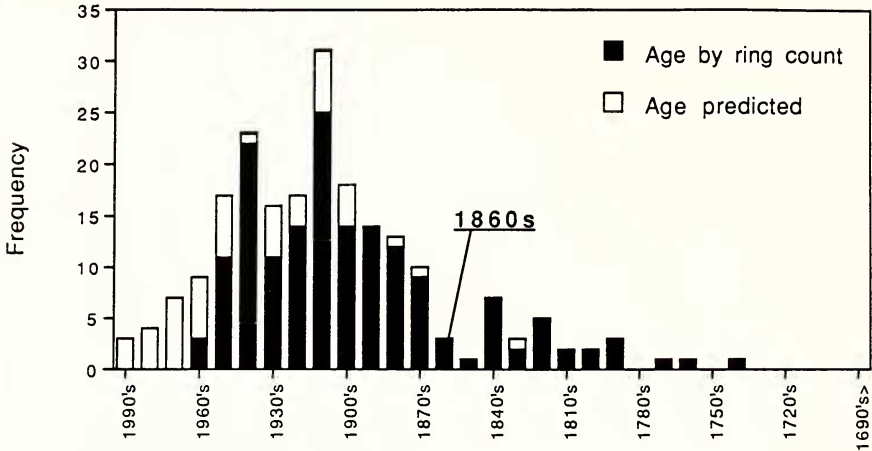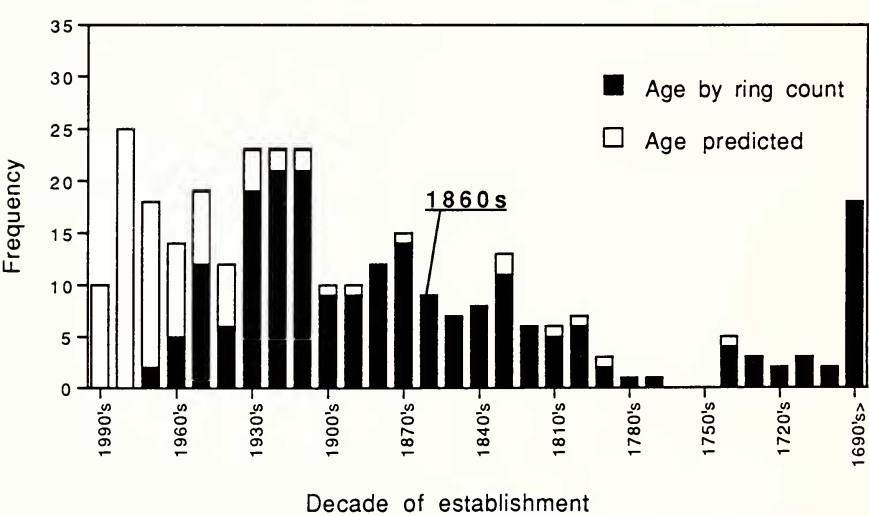**Figure 1a.   Tree establishment dates, high TRMI (mesic) sites.**

Figure 1b.   Tree establishment dates, low TRMI (xeric) sites.

Decade of establishment

FIGS. 1a, b.   Tree establishment dates of pinyon by decade, mesic (TRMI > 30) and xeric (TRMI < 30) sites along the lower montane treeline ecotone, Inyo and Mono Counties, California.

tree (0.5/ha) over 100 years old; and 92 years on xeric sites, with 33 trees (17 trees/ha) over 100 years. The average 41 year old pinyon today is about 125–150 cm tall, which is similar to the average shrub height in most of the plots. With 17/45 trees per hectare over 100 years old on xeric sites in 1861, ridges and slopes may have visually appeared as open, savanna-like stands consisting of predominantly mature, widely-spaced trees. Valley bottoms and draws may have appeared to be wholly absent of trees in 1861.

Both xeric and mesic sites have had considerable seedling recruitment since European settlement. In the last 135 years, estimated tree density has increased 400% on xeric sites and 800% on mesic

sites. This is consistent with early observations that lower montane woodlands were primarily restricted to topographic convexities prior to 1861, and that existing stands were formerly more open and contained largely mature trees. As pinyon cover has increased on all topographic settings, understory shrub, grass and herb cover has decreased. Current understory total vegetation cover in xeric sites is 14% on average, whereas mesic sites support 31% understory cover. While these values of understory cover may also reflect different soil moisture regimes and edaphic settings, and not simply relationships to woodland canopy cover or competition with pinyon, the negative relationship between understory vegetation cover and tree density or can-

TABLE 1. PINYON STAND DATA FOR XERIC AND MESIC SITES AT THE LMTE.*

	Number of trees		Tree density		Mean age (years)		Mature trees, 1861 (trees >100 years)	
	Current	1861	Current	1861	Current	1861	No.	Density
Xeric sites (TRMI < 30)	309	91	156/ha	45/ha	106.6	92	33	17/ha
Mesic sites (TRMI > 30)	212	28	107/ha	13/ha	83.6	41	1	0.5/ha
All sites	512	119	130.3/ha	29/ha	97.2	80	34	8.8/ha

* For all measures, stands on xeric sites are significantly different than mesic stands (p < 0.01).

opy cover is well-documented (Austin 1987; Everett and Koniak 1981; Pieper 1990).

At the larger scale of the entire elevational gradient of mountain ranges in the Great Basin, a coarse-grained view would show the altitudinal zonation of vegetation is largely influenced by effective soil moisture as determined by climatic variables, such as average precipitation and temperature (Daubenmire 1943; Billings 1951). However, a finer-grained view of the small scale topographic relationships along the LMTE suggests an inverse relationship of pinyon to topographically influenced moisture patterns. Greater pinyon stand development on xeric topographic settings along the LMTE is contrary to previous reports that montane tree species become increasingly restricted to mesic topographic settings towards the lower ecotone (Parker 1980; Peet 1988; Rourke 1988; Whittaker and Niering 1965). Two factors may have produced this inverse pattern: shrub and grass competition prior to 1861 may have excluded trees from the sites with deeper, finer-textured soils and more favorable moisture status; and, the greater density and biomass of shrubs and grasses may have supported more frequent fires, causing the mortality of invasive trees (Burkhardt and Tisdale 1969, 1976; Cottam and Stewart 1940; Blackburn and Tueller 1970). The introduction of livestock grazing in the West reduced competitive cover and fuel to carry fires, which may have allowed trees to become established, and then survive into maturity.

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